

## SHORT COMMUNICATION

# Relationship between body size and homing ability in the genus *Osmia* (Hymenoptera; Megachilidae)

CHRISTELLE GUÉDOT<sup>1</sup>, JORDI BOSCH<sup>2</sup> and WILLIAM P. KEMP<sup>3</sup><sup>1</sup>Biology Department, Utah State University, Logan, Utah, U.S.A., <sup>2</sup>CREAF – Ecologia, Universitat Autònoma de Barcelona, Bellaterra, Spain and <sup>3</sup>USDA-ARS, Red River Valley Agricultural Research Center, State University Station, Fargo, North Dakota, U.S.A.

**Abstract.** 1. The maximum homing ability of female bees, that is, their capacity to return to the nest after being displaced a certain distance, is considered to be an estimate of their maximum foraging distance.

2. The present study provides data on homing ability and body weight for *Osmia lignaria* and combines them with data for five other congeners, *O. rufa*, *O. cornuta*, *O. pedicornis*, *O. cornifrons*, and *O. emarginata* for analysis. These species are important pollinators of spring-flowering plants, and some have been developed as commercial crop pollinators.

3. It is shown that homing ability is positively and linearly related to body weight ( $r^2 = 0.81$ ;  $P = 0.01$ ).

4. These results should be of use in selecting *Osmia* species as potential crop pollinators and establishing adequate buffer distances around genetically modified crops.

**Key words.** Flight distance, foraging range, homing range, *Osmia*, pollen dispersal.

## Introduction

Bees are the primary pollinators of many crops and wild flowers, thus playing a critical role in gene flow via pollen dispersal. Gene flow among flower patches is of important relevance to in the current scenario of loss and fragmentation of natural habitats (Kearns *et al.*, 1998). Knowledge of foraging and drift ranges is also critical to understand the impact of pollen dispersal on the management of genetically modified crops in open fields, particularly in agricultural areas containing conventional crops (Scheffler *et al.*, 1993).

Nesting bees are central place foragers, returning to their nest several times a day for nest building and brood provisioning. Female bees must often fly long distances to collect pollen and nectar and, sometimes, nesting materials. The homing distance, or maximum distance from which bees are able to find their nest, is believed to be a good indicator of a species' maximum foraging range (van Nieuwstadt & Ruano Iraheta, 1996; Gathmann & Tschardt, 2002). Homing distance varies widely among bee species, from ~200 m in *Pithitis smaragdula* (Abrol & Kapil, 1994) to 23 km in *Euplusia surinamensis* (Janzen, 1971). Several studies report a positive correlation between body size and homing ability (Abrol & Kapil, 1994; van

Nieuwstadt & Ruano Iraheta, 1996; Gathmann & Tschardt, 2002; Greenleaf *et al.*, 2007), although absence of such a correlation has been reported for *Bombus* spp. (Knight *et al.*, 2005). A positive correlation between body size and homing ability has been attributed at least in part to the organism's energy requirements. Larger species have larger energy needs, requiring a larger home range to gather sufficient resources (McNab, 1963; Reiss, 1988). In addition, the shape of this relationship may be confounded by phylogenetic constraints and variation in life-history and behavioural traits among bee genera and families. For example, social species, which need to gather large amounts of pollen and nectar to feed an entire colony, are expected to have greater foraging ranges than solitary species. The outstanding homing ability of *Euplusia surinamensis* has been attributed to the species' need to fly long distances in a habitat with a highly patchy distribution of floral resources (Janzen, 1971).

*Osmia* are solitary bees, many of which nest in pre-established cavities (Cane *et al.*, 2007). In these cavities, females build linear series of cells that they provision with a nectar and pollen mixture (Torchio, 1989). *Osmia* are important pollinators of spring- and summer-flowering plants, and several species have been developed as pollinators of orchard, berry, and seed crops (Bosch *et al.*, 2008). The study of homing ability in *Osmia* has important ecological implications for pollen dispersal in fragmented landscapes and in agricultural ecosystems, especially as it relates to pollen transfer between genetically modified and conventional crops.

Correspondence: Christelle Guédot, USDA-ARS Yakima Agricultural Research Laboratory, 5230 Konnowac Pass Road, Wapato, WA 98951, U.S.A. E-mail: christelle.guedot@ars.usda.gov

**Table 1.** Number of *Osmia lignaria* females returning to the nesting site with average duration of return flights in relation to the distance from the release site to the nest.

	Distance from release site to nest (m)					
	600	800	1000	1200	1400	1600
Females displaced	10	10	10	10	10	10
Females returning	9	8	7*	7	0	0*
Duration (min)	44.2 ± 8.2	75.8 ± 8.1	91.4 ± 14.9	98.9 ± 9.9	–	–

\*One of the missing bees returned the following day.

The present paper explores the relationship between body size and homing ability in six species of *Osmia*. We are interested in confirming the positive relationship between these two parameters and in characterising this relationship.

## Materials and methods

Information on the homing ability of *O. emarginata*, *O. cornifrons*, *O. pedicornis*, *O. cornuta*, and *O. rufa* was obtained from the literature (Molitor, 1937; Kitamura & Maeta, 1969; Vicens & Bosch, 2000; Gathmann & Tschardt, 2002). We report the homing distance established in the respective studies (Molitor, 1937; Kitamura & Maeta, 1969 for *O. pedicornis*; Vicens & Bosch, 2000) or the distance at which at least 50% of bees returned to their nest (Kitamura & Maeta, 1969 for *O. cornifrons*; Gathmann & Tschardt, 2002).

The homing ability of *O. lignaria* was measured in a population released in an apple orchard near Logan, Utah, U.S.A., in May 2002. Females of this population were nesting in paper straws (14 cm long, 7.5 mm inside diameter) inserted in drilled solid wood blocks (width × height × depth = 14 × 14 × 13 cm) that were placed in a wood shelter (Torchio, 1982). Each nesting hole was provided with a paper straw. Actively nesting females returning with a pollen–nectar load and entering their nest without hesitation were selected. Before females departed for a new foraging trip, they were trapped inside the nesting paper straw and transported to predetermined locations, at distances of 600, 800, 1000, 1200, 1400, and 1600 m. Females inside the nests were briefly anaesthetised (<30 s) with CO<sub>2</sub>, extracted from the nest, marked on the thorax with enamel paint and allowed to fly

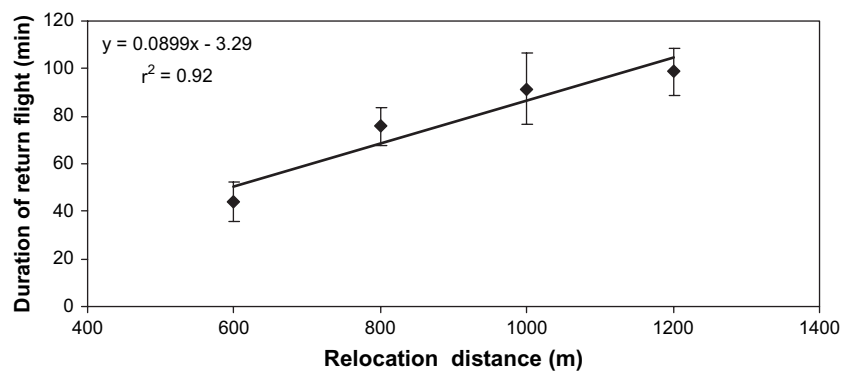
away. The paper straw nests were returned to the nesting site and inserted back into their original position in the nesting blocks prior to the resident bee's return. Nesting blocks were observed until females returned or for a maximum of 3 h. The time spent by females to return to the nesting site was recorded. Each female was exposed to only one capture–release treatment, with 10 females released at each location.

Body weight (in mg) of the six species was estimated from inter-tegular spans (in mm) of pinned specimens (Cane, 1987; dry weight = 1.972(inter-tegular span)<sup>2.43</sup>). Pinned specimens were obtained from the U.S. National Pollinating Insects Collection, in Logan, Utah. Data were submitted to simple linear regressions using the REG procedure of SAS 9.1 (SAS Institute Inc., 2003).

## Results

Most *O. lignaria* females displaced to distances shorter than 1200 m returned to their nest. Beyond 1200 m, no female returned to the nesting site within 3 h of displacement (Table 1). Time to return to the nesting site was positively correlated to relocation distance, following the linear regression:  $y = 0.090x - 3.290$  ( $n = 4$ ;  $F = 21.77$ ;  $r^2 = 0.92$ ;  $P = 0.04$ ), where  $y$  is the duration of return flight and  $x$  is the distance from the release site (Fig. 1).

Estimated dry weights of the six *Osmia* species are shown in Table 2. Homing ability showed a positive relationship with body size. This relationship was linear:  $y = 54.526x - 866.63$ , where  $y$  is the homing ability distance (m) and  $x$  is the dry weight (mg) ( $n = 6$ ;  $F = 16.82$ ;  $r^2 = 0.81$ ;  $P = 0.01$ ) (Fig. 2).

**Fig. 1.** Relationship between duration of return flights of *Osmia lignaria* females and distance from release site to nest.

**Table 2.** Mean ( $\pm$ SE) female dry weight and homing distance of six *Osmia* species.

	<i>n</i>	Dry weight (mg)	Homing distance (m)	References
<i>O. cornifrons</i>	30	22.2 $\pm$ 0.8	500*	Kitamura and Maeta (1969)
<i>O. rufa</i>	30	27.0 $\pm$ 1.0	500*	Gathmann and Tschardtke (2002)
<i>O. pedicornis</i>	12	33.0 $\pm$ 2.8	700	Kitamura and Maeta (1969)
<i>O. lignaria</i>	30	33.5 $\pm$ 1.1	1200	Present study
<i>O. emarginata</i>	1	38.7	1000	Molitor (1937)
<i>O. cornuta</i>	30	45.5 $\pm$ 1.9	1800	Vicens and Bosch (2000)

\*Distance at which at least 50% of bees returned to their nest.

## Discussion

Central-place foragers tend to forage near the nest surroundings, provided floral resources are present. As resources become scarcer in the nest vicinity, they expand their foraging range (Schneider & McNally, 1993; Steffan-Dewenter & Kuhn, 2003). This study shows that increasing the distance between the nest and the release location eventually led to a decrease in the proportion of *O. lignaria* females that returned to the nest, establishing the homing distance of *O. lignaria* females at 1200 m. Sudden drops in homing ability beyond a certain distance have been obtained with other bee species (Rau, 1929; Roubik & Aluja, 1983; Abrol & Kapil, 1994; van Nieuwstadt & Ruano Iraheta, 1996; Chmurzyński *et al.*, 1998; Vicens & Bosch, 2000; Goulson & Stout, 2001).

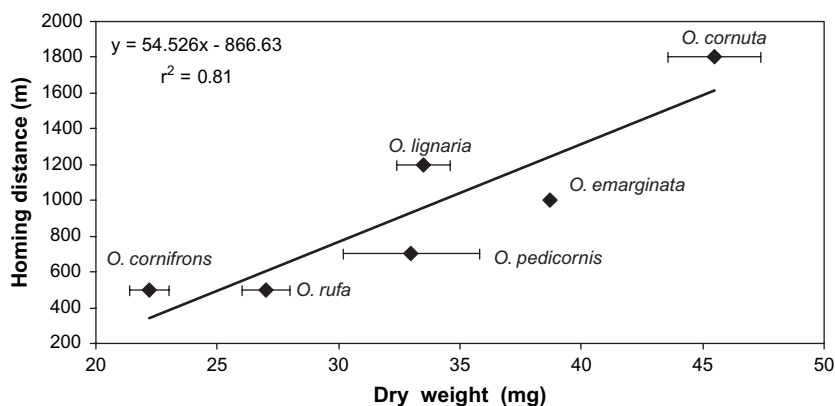
*Osmia lignaria* females spent more time returning to the nest when relocation distances were increased, which was consistent with previous studies on *O. rufa* and *O. cornifrons* (Kitamura & Maeta, 1969; Gathmann & Tschardtke, 2002). On the other hand, the variability of return times in *O. cornuta* did not reveal a correlation with distance, as a significant number of bees foraged on their way back to the nest (Vicens & Bosch, 2000). Absence of correlation was also reported in *Bombus terrestris* (Goulson & Stout, 2001). Return times may be influenced by several factors, such as motivational state of the bee to forage before reaching the nest, landmark availability, time and/or likelihood of encountering familiar landscape, and experience of the surrounding terrain (Southwick & Buchmann, 1995; Capaldi & Dyer, 1999).

It has been suggested that homing distance can provide an estimate of the maximum foraging range (van Nieuwstadt &

Ruano Iraheta, 1996; Gathmann & Tschardtke, 2002). Homing ability is determined on a single return to the nest from the release site, while foraging range includes both outbound and inbound flights from the nest to the resource. Homing ability should thus encompass foraging range. Based on this rationale, van Nieuwstadt and Ruano Iraheta (1996) showed that the foraging range of several stingless bee species was  $\sim$ 300 m shorter than their homing distance. On the other hand, homing distance might be underestimated if bees are artificially translocated to an unfamiliar environment.

The homing ability of a pollinator should also provide an estimate of its potential habitat size. Foraging range is probably less reliable in estimating habitat size, as it is dependent on multiple factors, such as distribution of resources (Schneider & McNally, 1993), availability of the resources during the season, or structure of the landscape (Steffan-Dewenter & Kuhn, 2003). For example, the homing distance of *O. cornuta* is 1800 m, but with abundant floral resources (peak orchard bloom), most females forage within 100–200 m of their nests (Vicens & Bosch, 2000).

Determining the homing ability of pollinators used in commercial farming could help better ascertain the optimum distribution of nesting shelters and release sites for commercial pollinator populations, as well as the distance of adequate habitat refugia for bees after crop harvest. When commercial bee populations, e.g. *Megachile rotundata* populations, are released in agroecosystems, a large proportion of the females do not nest at their release site, but rather drift among the various release sites (Bosch & Kemp, 2005). Drift, which is suggested to increase with body size, is also likely to be correlated to homing ability (Tschardtke & Brandl, 2004).



**Fig. 2.** Relationship between dry weight and homing distance in six *Osmia* species. Standard error bars are not given for species with a sample of 1. The homing distance established in the respective studies is reported for *O. lignaria*, *O. emarginata*, *O. pedicornis*, and *O. cornuta*. With *O. cornifrons* and *O. rufa*, the distance at which at least 50% of bees returned to their nest is reported.

The results of the present study confirm that homing ability is correlated to body size in *Osmia*, as found in previous studies (Abrol & Kapil, 1994; van Nieuwstadt & Ruano Iraheta, 1996; Gathmann & Tschamtkke, 2002; Greenleaf *et al.*, 2007). Furthermore, the results of the present study suggest that this relationship is linear in *Osmia*. Phylogenetic and/or behavioural constraints may confound the shape of this relationship. For example, oligolectic (pollen specialist) bees have been hypothesised to have greater foraging ranges than polylectic bees, which can forage on a wider array of plants (Gathmann & Tschamtkke, 2002; Greenleaf *et al.*, 2007). To minimise the potential effect of these constraints, the six species considered in the present study belong to the same subgenus, *Osmia* (*Osmia*), which was found to be monophyletic based on both molecular and behavioural characters, and are known to be polylectic (Bosch *et al.*, 2001). Homing abilities of other *Osmia* species can now be estimated by measuring their body size. These results should be of interest in selecting *Osmia* species as potential crop pollinators and establishing adequate buffer distances around genetically modified crops.

## Acknowledgements

We are grateful to P. Rieger and G. Trostle for their assistance throughout this study, and T. Griswold and O. Messinger for their help in measuring bees. Comments from J. Cane and T.L. Pitts-Singer as well as two anonymous reviewers were greatly appreciated.

## References

- Abrol, D.P. & Kapil, R.P. (1994) On homing ability and pollination effectiveness of bees. *Mysore Journal of Agricultural Sciences*, **28**, 249–252.
- Bosch, J. & Kemp, W.P. (2005) Alfalfa leafcutting bee population dynamics, flower availability, and pollination rates in two Oregon alfalfa fields. *Journal of Economic Entomology*, **98**, 1077–1086.
- Bosch, J., Maeta, Y. & Rust, R. (2001) A phylogenetic analysis of nesting behavior in the genus *Osmia* (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, **94**, 617–627.
- Bosch, J., Sgolastra, F. & Kemp, W.P. (2008) Life cycle ecophysiology of *Osmia* mason bees used as crop pollinators. *Bee Pollination in Agricultural Ecosystems* (ed. by R. R. James and T. L. Pitts-Singer), pp. 83–104. Oxford University Press, Oxford.
- Cane, J.H. (1987) Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society*, **60**, 145–147.
- Cane, J.H., Griswold, T. & Parker, F.D. (2007) Substrates and materials used for nesting by North American *Osmia* bees (Hymenoptera: Apoidea: Megachilidae). *Annals of the Entomological Society of America*, **100**, 350–358.
- Capaldi, E.A. & Dyer, F.C. (1999) The role of orientation flights on homing performance in honeybees. *Journal of Experimental Biology*, **202**, 1655–1666.
- Chmurzyński, J.A., Kieruzel, M., Krzysztofiak, A. & Krzysztofiak, L. (1998) Long-distance homing ability in *Dasygaster alterator* (Hymenoptera, Megachilidae). *Ethology*, **104**, 421–429.
- Gathmann, A. & Tschamtkke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757–764.
- Goulson, D. & Stout, J.C. (2001) Homing ability of the bumble bee *Bombus terrestris* (Hymenoptera: Apidae). *Apidologie*, **32**, 105–111.
- Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.
- Janzen, D.H. (1971) Euglossine bees as long-distance pollinators of tropical plants. *Science*, **171**, 203–205.
- Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998) Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics*, **29**, 83–112.
- Kitamura, T. & Maeta, Y. (1969) Studies on the pollination of apple by *Osmia*: (III) Preliminary report on the homing ability of *Osmia cornifrons* (Radoszkowski) and *O. pedicornis* Cockerell. *Kontyû*, **37**, 83–90.
- Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, R.A. *et al.* (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, **14**, 1811–1820.
- McNab, B.K. (1963) Bioenergetics and the determination of home range size. *American Naturalist*, **97**, 133–140.
- Molitor, A. (1937) Zur vergleichenden Psychobiologie der akuleaten Hymenopteren auf experimenteller Grundlage. *Biologia Generalis*, **13**, 294–333.
- van Nieuwstadt, M.G.L. & Ruano Iraheta, C.E. (1996) Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie*, **27**, 219–228.
- Rau, P. (1929) Experimental studies in the homing of carpenter and mining bees. *Journal of Comparative Psychology*, **9**, 35–70.
- Reiss, M. (1988) Scaling of home range size: body size, metabolic needs and ecology. *Trends in Ecology & Evolution*, **3**, 85–86.
- Roubik, D.W. & Aluja, M. (1983) Flight ranges of *Melipona* and *Trigona* in tropical forest. *Journal of the Kansas Entomological Society*, **56**, 217–222.
- SAS Institute Inc. (2003) *SAS/STAT User's guide, Version 9.1*. SAS Institute Inc., Cary, NC.
- Scheffler, J.A., Parkinson, R. & Dale, P.J. (1993) Frequency and distance of pollen dispersal from transgenic oilseed rape (*Brassica napus*). *Transgenic Research*, **2**, 356–364.
- Schneider, S.S. & McNally, L.C. (1993) Spatial foraging patterns and colony energy status in the African honey bee, *Apis mellifera scutellata*. *Journal of Insect Behavior*, **6**, 195–210.
- Southwick, E.E. & Buchmann, S.L. (1995) Effects of horizon landmarks on homing success in honey bees. *American Naturalist*, **146**, 748–764.
- Steffan-Dewenter, I. & Kuhn, A. (2003) Honeybee foraging in differentially structured landscapes. *Proceedings of the Royal Society of London, Series B*, **270**, 569–575.
- Torchio, P.F. (1982) Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson in apple orchards: I, 1975 studies (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, **55**, 136–144.
- Torchio, P.F. (1989) In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America*, **82**, 599–615.
- Tschamtkke, T. & Brandl, R. (2004) Plant–insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405–430.
- Vicens, N. & Bosch, J. (2000) Nest site orientation and relocation of populations of the orchard pollinator *Osmia cornuta* (Hymenoptera: Megachilidae). *Environmental Entomology*, **29**, 69–75.

Accepted 16 July 2008

First published online 24 September 2008